IMPLICATIONS OF THE PHYLOGENY OF PIMOIDAE FOR THE SYSTEMATICS OF LINYPHIID SPIDERS (ARANEAE, ARANEOIDEA, LINYPHIIDAE)

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The araneoid family Pimoidae (new rank) is hypothesized to be the sister group of Linyphiidae. *Louisfagea* Brignoli is a junior synonym of *Pimoa* Chamberlin and Ivie (new synonymy). The characters that support the monophyly of Pimoidae and of Linyphiidae plus Pimoidae are discussed. Explicit outgroup comparison to the closest relatives of linyphiids (i.e., pimoids) allows studies of character evolution and character polarization within linyphiids and the assessment of previous phylogenetic hypotheses for the family. Preliminary data on the implications of pimoid phylogeny for linyphiid systematics are evaluated, based mainly on morphological characters. Linyphiid monophyly is discussed.

La familia araneoide Pimoidae (nuevo rango) es, hipotéticamente, el grupo hermano de Linyphiidae. El género *Louisfagea* Brignoli se considera sinónimo de *Pimoa* Chamberlin and Ivie (nueva sinonimia). Se discuten los caracteres que apoyan la monofilia de Pimoidae y de Linyphiidae más Pimoidae. La utilización explícita del criterio de comparación con el grupo externo de los linífidos (es decir, los pimóidos) permite estudiar la evolución y polarización de caracteres en linífidos, así como la evaluación de anteriores hipótesis filogenéticas sobre esta familia. Se evaluan los datos preliminares, basados en caracteres morfológicos principalmente, sobre las implicaciones de la filogenia de los pimóidos para la sistemática de los linífidos. También se discute la monofilia de Linyphiidae. □*Pimoidae, Linyphiidae, Pimoa, cladistics, phylogeny, monophyly, homology.*

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Linyphiids are one of the dominant spider groups in the Holarctic region. Despite their overwhelming diversity and involved taxonomic history the phylogenetic structure of the family and their relationship to other araneoids are very poorly understood. In this paper I present some preliminary data on the systematics of pimoids, confirming their sister-group relationship to linyphiids, and on the cladistic structure of a small sample of linyphiid genera. A revision and numerical cladistic analysis of the pimoids and the sample of linyphiid taxa (Hormiga, in press), together with detailed character information, will be published elsewhere shortly. The study of the phylogeny of the pimoids requires the inclusion of at least a sample of linyphiids (their putative sister-group) in order to assess character state polarities by means of outgroup comparison. It is in such a context that the present study should be considered, since the small sample of genera used here can by no means account for the whole range of linyphiid diversity. However, quantitative cladistic analysis of the data presented here enables for some testable hypotheses on linyphiid systematics and character evolution, by explicitly stating phylogenetic relationships in terms of synapomorphies rather than by the more speculative approaches that have commonly been used in traditional linyphiid higher systematics. This approach enables us to evaluate comparative morphological data (or any other kind of biological data) in a cladistic context. Hypotheses on phylogeny and character homology hypotheses are indistinguishable because 'every hypothesis of homology is a hypothesis of monophyletic grouping' (Patterson, 1982). Finally, the present study allows for a preliminary test of the phylogeny of the linyphiid subfamilies proposed by Wunderlich (1986).

MATERIALS AND METHODS

Taxa

Nine linyphiid, five pimoid, and two non-linyphiid araneoid genera that are possible outgroups of the pimoid-linyphiid complex are used in this study. The linyphiid taxa selected represent the subfamilies and tribes used by Wunder-

lich (1986) in his phylogenetic scheme for Linyphiidae (given here in parentheses): *Linyphia triangularis* (Clerck) and *Microlinyphia dana* (Chamberlin and Ivie)(Linyphiinae, Linyphiini); *Bolyphantes luteolus* (Blackwall) and *Lepthyphantes tenuis* (Blackwall)(Linyphiinae, Micronetini); *Erigone psychrophila* Thorell and *Walckenaeria directa* (O.P.-Cambridge) (Erigoninae); *Haplinis diloris* (Urquhart) and *Novafroneta vulgaris* Blest (Mynogleninae); and *Stemonyphantes blauveltae* Gertsch (Stemonyphantinae). The pimoids (which contain 21 species, including 11 new species (Hormiga, in press) are represented here by five species: *Pimoa* (=*Louisfagea*) *rupicola* (Simon), *P.* (=*Louisfagea*) *crispa* (Fage), *P. altioculata* (Keyserling), *P. breviata* Chamberlin and Ivie, and *P. curvata* Chamberlin and Ivie. *Tetragnatha versicolor* Walckenaer and *Zygiella x-notata* (Clerck) are used as outgroups of the pimoid-linyphiid clade. The affinities of *Zygiella* are problematic: the genus is currently placed in Tetragnathidae, although not long ago it was thought to belong in Araneidae. Recent analyses of Araneoidea relationships by Coddington and Scharff suggest that *Zygiella* is either sister to Araneidae or Araneinae, i.e. it is the most basal taxon within araneids or basal within the araneine clade (Scharff and Coddington, pers. comm.).

Taxonomic note: I have used taxonomic decisions that will be soon discussed in greater detail elsewhere. The Pimoinae Wunderlich are raised to familial status (Pimoidae, NEW RANK) and are therefore removed from the Linyphiidae. Treating pimoids as a linyphiid subfamily produces a great change in the diagnosis of Linyphiidae, since it is largely based in male genitalic characters which are absent in the Pimoidae (e.g., intersegmental paracymbium, loss of the araneoid conductor, loss of the araneoid median apophysis, presence of a radix and a column, etc.). Once it is established that pimoids and linyphiids are sister-groups, the assignment of ranks is arbitrary. The exclusion of pimoids renders Linyphiidae more homogeneous and easier to diagnose. *Louisfagea* Brignoli, as presently defined, is polyphyletic (Hormiga, in press). The removal of *crispa* would leave the remaining species of *Louisfagea* as a paraphyletic genus. *Louisfagea* is regarded here as a junior synonym of *Pimoa* Chamberlin and Ivie (NEW SYNONYMY). Throughout this paper the taxon name Linyphiidae (linyphiids) does not include the pimoids.

Characters

The data set contains 47 characters (Table 1): 33 male and female genitalic characters, 5 spinneret spigot characters, 7 other morphological somatic characters, and 2 behavioral characters. The data consist mostly of original observations, but a few characters have been extracted from the literature. Although this data set integrates information from several character systems, it especially focuses on male palp and spinneret spigot morphology. The methods of study and of homology assessment of spinneret spigot morphology follow those of Coddington (1989). The work on linyphiid morphology (including the descriptive studies on male palp, spinneret spigot, and tracheal system morphology) will also be published elsewhere.

Analysis

The data set was analyzed using the computer program for phylogenetic analysis Hennig86 ver. 1.5 (Farris, 1988). Multistate characters were treated as non-additive (unordered).

RESULTS

Characters

Character distributions are summarized in Table 1. The desmitracheate tracheal system (*sensu* Millidge, 1984; character 35) is a synapomorphy of the erigonine clade. I have not been able to confirm some of the tracheal morphologies described by Millidge (1986). I have examined the tracheal system of several erigonine genera (*Erigone aletris* Crosby and Bishop, *E. psychrophila*, *Gonatium rubens* (Blackwall), *Grammonota angusta* Dondale, and *Hypselistes florens* (O.P.-Cambridge)) and have not found evidence of the median tracheae open-

TABLE 1. Rows represent characters and columns taxa. The first state is 'state 0', the second is 'state 1', etc. '?' represents missing data, and '—' non-applicable states. The last two columns give the consistency index (CI) and the weight (W) assigned to the character in the successive character weighting analysis (see text). Taxon numbers: 0 = *Tetragnatha versicolor*, 1 = *Zygiella x-notata*, 2 = *Linyphia triangularis*, 3 = *Microlinyphia dana*, 4 = *Bolyphantes luteolus*, 5 = *Lepthyphantes tenuis*, 6 = *Erigone psychrophila*, 7 = *Walckenaeria directa*, 8 = *Haplinis diloris*, 9 = *Novafroneta vulgaris*, 10 = *Stemonyphantes blauveltae*, The remaining taxa are species of *Pimoa*: 11 = *rupicola*, 12 = *crispa*, 13 = *altioculata*, 14 = *breviata*, 15 = *curvata*. Characters: 1-30, male genitalia; 31-33, female genitalia; 34-40, somatic morphology; 41-45, spinneret spigot morphology; 46, 47, behaviour.

		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	CI	W
1	Cymbium morphology: without dorsoectal denticulated process (DDP); with DDP	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
2	DDP denticles: numerous (20); few (<20)	—	—	—	—	—	—	—	—	—	—	—	0	0	1	1	1	1.00	10
3	Pimoid cymbial sclerite (PCS): absent; present	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
4	PCS -cymbium connection: sclerotized, rigid; membranous, flexible	—	—	—	—	—	—	—	—	—	—	—	0	1	1	1	1	1.00	10
5	PCS membranous ridge: absent; present	—	—	—	—	—	—	—	—	—	—	—	1	0	0	0	0	1.00	10
6	PCS shape: U; elongated anteroposteriorly; reversed J	—	—	—	—	—	—	—	—	—	—	—	0	2	1	1	1	1.00	10
7	Paracymbium attachment:integral; intersegmental	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
8	Paracymbium morphology: straight; large-pointed apex; U or J; linguiform-fused to PCS; triangular; short-procurved; *St* type	0	1	3	3	3	3	3	3	3	3	2	4	6	5	5	5	1.00	10
9	Paracymbium apophyses: present; absent	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0.50	3
10	Petiole:otherwise; fused to subtegulum	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
11	Tegular suture: conspicuous; subtle or absent	—	—	—	—	—	—	—	—	—	—	—	0	0	1	1	1	1.00	10
12	Mynoglenine tegular apophysis: absent; present	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1.00	10
13	Suprategulum: absent; fused; articulated	0	0	1	1	1	1	1	1	0	0	2	0	0	0	0	0	1.00	10
14	Median apophysis: present; absent	1	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0.33	3
15	Conductor: present; absent	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1.00	10
16	Conductor form: small and undivided; large and bilobate	0	0	—	—	—	—	—	—	—	—	—	0	0	0	1	1	1.00	10
17	Embolus length: long and filiform; short	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0.50	2
18	Embolic membrane: absent; present	—	0	1	0	1	1	1	1	1	1	0	—	—	—	—	—	0.50	2
19	Pimoid embolic process (PEP): absent; present	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
20	PEP conformation: undivided; divided	—	—	—	—	—	—	—	—	—	—	—	1	0	0	0	0	1.00	10
21	PEP base: narrow; wide and lamelliform	—	—	—	—	—	—	—	—	—	—	—	0	0	1	1	1	1.00	10
22	Radix: absent; present	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
23	Column (distal haematodocha): absent; present	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
24	Fickert's gland: absent; present	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1.00	10
25	Terminal apophysis: absent; present	—	0	1	1	1	1	1	0	0	0	0	—	—	—	—	—	0.50	3
26	Lamella characteristica: absent; present	—	0	1	1	1	1	0	0	0	0	0	—	—	—	—	—	1.00	10
27	♂pedipalpal tibial apophysis: absent; dorsal, rounded; retrolateral; ventral	0	0	0	0	0	0	2	2	0	0	3	1	1	1	1	1	1.00	10
28	♂ pedipalp tibial spines: not clustered; distal row	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1.00	10
29	Prolateral trichobothria in male palpal tibia: two; one	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0.50	4
30	Retrolateral trichobothria in ♂ palpal tibia: 2; 4; 3;>4	1	0	2	0	0	0	0	0	2	0	0	2	2	2	2	2	0.50	3
31	Epigynum form protrudes: less than its width; more	—	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1.00	10
32	Dorsal plate of epigynum, projections: absent; present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1.00	10
33	Atrium: absent; present	—	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0.50	2
34	Mynoglenine cephalic sulci: absent; present	0	0	0	0	0	0	?	0	1	1	0	0	0	0	0	0	1.00	10
35	Tracheal system: haplotrachcate; desmitracheate	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1.00	10
36	Ectal chelicerae of ♂: smooth; with stridulatory striae	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0.33	1
37	Retrolateral teeth ♀ chelicera: 3; >3; 2	0	0	1	1	1	1	1	0	1	1	?	2	0	?	2	2	0.50	5
38	♀ pedipalpal tarsal claw: present; absent	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0.50	2
39	Leg autospasy: otherwise; at patella-tibia	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
40	Trichobothrium metatarsus 1V: present; absent	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0.50	3
41	PMS: with anterior aciniform brush; without	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
42	Aciniform spigots in ♀ PMS: > 1; 1; absent	0	0	0	0	0	0	0	0	0	0	2	2	1	2	2	2	0.66	10
43	PLS mesal cylindrical spigot base: same size; enlarged	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
44	PLS aciniform field: random spigots; elongated field	1	0	1	1	1	1	1	1	1	1	1	—	—	—	—	—	1.00	10
45	Aciniform spigots in ♀ PLS: >1; 1; absent	0	0	0	0	0	0	0	0	0	0	2	1	1	2	2	2	0.66	10
46	♂spins sperm web while: above sperm web; below it	?	?	0	0	?	0	1	?	1	?	?	?	?	?	?	?	1.00	10
47	♂ position during ejaculation: above sperm web; below	?	?	0	0	?	0	1	?	1	?	?	?	?	?	?	?	1.00	10

ing directly to separate spiracles, as Millidge reported. The mentioned erigonines posses a tracheal atrium (*contra* Millidge, 1986:57), which, using an aqueous solution of chlorazol black, stains similarly to the rest of the tracheal system. The spiracle is most visible at both ends, where it is wider and rounded, although there is a slit connecting both ends. Such ends are not a closed circle (i.e., they are not separate spiracles), as Millidge's illustrations seem to suggest (e.g. his figure 5), since they are open at its inner part to the interconnecting slit. *Stemonyphantes blauveltae* and *Allomengea pinnata* (Emerton) have tracheal atria opening through a single spiracle, contrary to Millidge's assertion that in both genera the atrium opens via two spiracles. Atria opening via a single spiracle were also found in *Drapetisca alteranda* Chamberlin, *Centromerus sylvaticus* (Blackwall), *Lepthyphantes flavipes* (Blackwall), *L. tenuis* (Blackwall), and *L. intricatus* (Emerton). These latter genera were also reported by Millidge (the first one only implicitly) to have the atrium opening via two spiracles. In the two latter species the slit is very similar to the one reported here for the erigonines, with markedly wider round ends (this fact might have caused them to be taken as having two spiracles).

The spinneret spigot morphology characters (41-45) support the monophyly of the pimoids and of the pimoid-linyphiid clade (Hormiga, in press). Linyphiid and pimoid spigot morphology is consistent with the araneoid groundplan (Coddington, 1990b; Peters and Kovoor, 1991; Hormiga, in press). The pimoid-linyphiid clade lacks the PMS aciniform brush found in primitive orbicularians (character 41), but so do many tetragnathids and the theridiids. Pimoids and linyphiids share the position of the mesal cylindrical spigot on the periphery of the PLS, but this is not exclusive to the pimoid-linyphiid clade: it is also found in *Zygiella x-notata* (pers. observ.) and in some other tetragnathids (Coddington, pers. comm.; Platnick *et al.*, 1990). An enlargement of the base of the peripheral cylindrical spigot of the PLS (character 43) is characteristic of pimoids and linyphiids. Pimoids have drastically reduced the PMS and PLS aciniform fields (characters 42 and 45): they either have one or none aciniform spigots on each spinneret. *Stemonyphantes* has also lost, presumably in parallel, the aciniform spigots in both the PMS and the PLS.

The use of the mating sequence and the transfer of sperm (characters 46-47) as taxonomic characters in linyphiids was studied by van Helsdingen (1965, 1969, 1983). Blest and Pomeroy (1978) studied the sexual behavior of *Haplinis diloris*. I have used data from van Helsdingen's observations as valid for the different species of *Lepthyphantes* and *Microlinyphia* in my data, under the assumption that there is no variation for the characters under study at the intrageneric level. For *Erigone psychrophila*, I have also used data from other species in the same genus, namely *E. dentipalpis* and *E. longipalpis* (Gerhardt (1927, 1923) cited in van Helsdingen (1983)). The male position during the construction of the sperm web (fork and web) and during ejaculation is below the sperm web in erigonines and mynoglenines, and above (only the web, the fork is constructed from below) in Linyphiini and Micronetini.

Analysis

The data (Table 1) were analyzed using the implicit enumeration option of Hennig86, which found four equally parsimonious cladograms with a length of 81 steps and consistency and retention indices of 0.74 and 0.81 respectively. These four topologies differ in the interrelationships of pimoids and in the position of *Stemonyphantes*, which in one of the four cladograms is sister to the pimoids. This latter topology is the result of the parallel loss of the aciniform fields in pimoids and linyphiids. Deactivating the characters that account for the number of aciniform spigots in the PMS and PLS (42 and 45, respectively) and using the implicit enumeration option three cladograms are obtained. These three cladograms are the same as those obtained with the 'active' characters, with the exclusion of the topology that clusters *Stemonyphantes* with pimoids. Successive character weighting (Farris, 1969; Carpenter, 1988) was used, as implemented by Hennig86, to choose a cladogram from the set of four equally parsimonious cladograms. A single iteration produced one cladogram (Fig. 1), which corresponds to one of the original set of four. This result is stable in a second iteration. Because this cladogram is based on the most consistent characters it is preferred as a hypothesis for explaining the relationships of this sample of taxa. The cladistic analysis of this selection of pimoid taxa produces results (i.e. tree topologies) fully congruent with those obtained in Hormiga (in press), in which a total of 20 pimoid species were analyzed together with the same sample of linyphiids and the two outgroup genera.

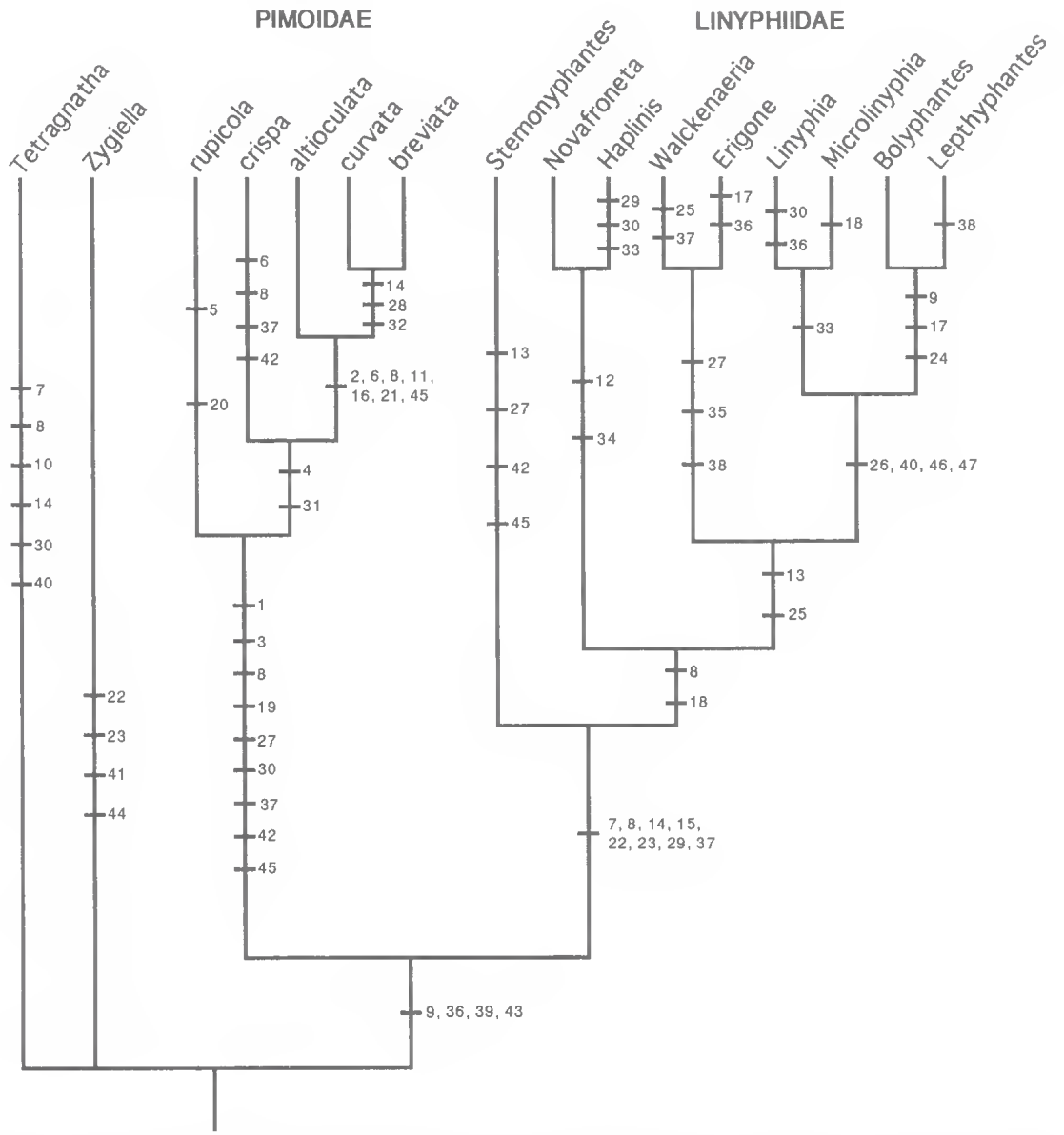

FIG. 1. Preferred minimum length cladogram for the taxa and characters in Table 1 (three equally parsimonious alternative topologies exist; see text). The cladogram length is 81 steps; the consistency and retention indices are 74 and 81, respectively.

DISCUSSION

Monophyly of the Pimoid-Linyphiid Clade

Pimoids and linyphiids emerge as a monophyletic assemblage, unambiguously supported by the presence of cheliceral stridulatory striae, patellar autospasy, and the enlargement of the peripheral cylindrical spigot base in the PLS. Paracymbial apophyses are secondarily absent (i.e. lost) in the pimoid-linyphiid clade, although they are regained in the Micronetini. All these characters (except the patellar autospasy) exhibit some degree of homoplasy.

Millidge (1988) rejected the inclusion of Linyphiidae in Araneoidea, and instead related them to Agelenidae (*s. lat.*), Amphinectidae, and

other taxa currently placed in Amaurobioidea and Dictynoidea. His hypothesis on the exclusion of linyphiids from Araneoidea has been elegantly rebutted by Coddington (1990b), who stated that linyphiids exhibit 9 out of the 10 synapomorphies that support the monophyly of Araneoidea. Pimoids share the same 9 araneoid synapomorphies. Peters and Kovoor (1991) studied the structure, histochemistry, and function of the spinning apparatus of *Linyphia triangularis* and concluded that the data did not provide any indication of close relationship between Linyphiidae and Agelenidae. Certainly Millidge's hypothesis lacks character support. The available data clearly argue in favor of the inclusion of the pimoid-linyphiid clade in Araneoidea. Furthermore, Millidge's idiosyncratic method of phylogenetic inference is flawed because, among other things, it seems to suggest the use of symplesiomorphies (by 'reversing' the outgroup comparison method) to establish family relationships (p. 254). It is well known that grouping by plesiomorphic character states produces paraphyletic groups (Hennig, 1966) and therefore should be avoided.

A major problem in araneoid phylogeny is the placement of the theridiid and the linyphiid-pimoid lineages, in which the orb web architecture has been lost (Coddington and Levi, 1991). Cyatholipidae have been suggested as another possible sister group of linyphiids (Coddington, 1990a). While the sheet web might support this hypothesis, the evidence provided by the morphological data is, at the moment, inconclusive.

Monophyly of Pimoids

Pimoid monophyly is supported by nine synapomorphies, six of them from male palpal morphology and two from spigot morphology. It is interesting to note that none of the pimoid-linyphiid synapomorphies refer to palpal morphology, which is quite different in these two lineages and might reflect a very old time of divergence and/or a rapid rate of character change for the male genitalia. The highly derived spigot morphology of pimoids is unique among araneoids. With the exception of *Stemonyphantes* no other araneoids have been reported to loose all the aciniform gland spigots.

Monophyly, Character Analysis, and Cladistic Structure of Linyphiids

Linyphiid monophyly is supported by eight synapomorphies. Seven of these eight characters (i.e. all except character 8) are homoplasious. With the increasing number of studies that use quantitative cladistic methods it is becoming clear that homoplasy is quite common (Coddington and Levi, 1991). Coddington (1990b) noted that many of the most useful characters for the inference of araneomorph phylogeny were homoplasious. Griswold (in press), in his study of the Lycosoidea, arrived at a similar conclusion for female genitalic characters. Linyphiids are not an exception, and this fact will not surprise most linyphiid taxonomists. For example, intersegmental paracymbia (character 7), similar to the linyphiid type, are also found in *Tetragnatha* and *Pachygnatha* (Levi, 1981:274, 286). Millidge (1988:258) considers the two latter cases as integral paracymbia, different from the linyphiid type, in which case the homoplasy would be removed from this character. But regardless of possible instances of homoplasy, the intersegmental paracymbium is a putative synapomorphy for linyphiids. Coding the paracymbial morphology (character 8) is not an easy task. I have taken a conservative approach by coding it with a high number of character states (seven), in part due to the high morphological diversity of this structure. The coding used produced no extra length (the character's consistency index is 1), but by itself it provides little grouping information (only two states occur in more than one taxon). The states are thus 'ordered' by the tree topology generated by all characters (the final optimization of the character on the cladogram was done by hand, because several equally parsimonious optimizations exist). Blest (1979) and Wunderlich (1986) consider that mynoglenines and erigonines share the same type of paracymbium ('simple paracymbium'). Van Helsdingen (1986:122) argued against this view by pointing out that many linyphiine genera also have the so-called 'simple' paracymbium. Although in some cases erigonines and mynoglenines seem to have morphologically 'simpler' paracymbia (short proximal and distal branches, sometimes J-shaped, without apophyses) than some of the linyphiini and micronetini, I cannot see a clear-cut distinction between these two states. I have coded all the linyphiids (except *Stemonyphantes*) as having the same overall paracymbium morphology (with a proximal and a distal branch of varying length and being more or less J or U-shaped). The paracymbium type found in *Stemonyphantes* is considered by Millidge (1988) as an intermediate form between the integral and intersegmental types. This latter type of paracymbium is inferred to be the primitive state for

linyphiids. This state is subsequently transformed into the paracymbium morphology found in the rest of linyphiids. Coding mynoglenines and erigonines as sharing the same unique character state (i.e., the 'simple' paracymbium), as Blest and Wunderlich have suggested, produces no changes in the cladogram topology.

The presence of a median apophysis and a conductor on the tegulum is regarded as plesiomorphic for araneoids (Coddington, 1990a). Pimoids have a conductor and a median apophysis (Hormiga, in press). The absence in linyphiids of a true (i.e. tegular) conductor and a median apophysis (Coddington, 1990a) are regarded as synapomorphies for linyphiids (characters 15 and 14, respectively). Two potential synapomorphies of linyphiids, the radix and the column, are waiting for resolution of the outgroup of the pimoid-linyphiid clade in order to be tested. The linyphiid radix (character 22) might be homologous to the araneid radix, and therefore plesiomorphic for linyphiids, if araneids are the sister group of pimoid-linyphiids (Coddington, 1990a). The same happens with the linyphiid column or stalk (*sensu* Saaristo, 1971; character 23) that connects the radix to the tegulum/suprategulum. The column could be homologous to the distal haematodocha if araneids are sister to the pimoid-linyphiid clade (Coddington, 1990a). If that is not the case, the homology of the linyphiid radix and column with its presumed equivalents in Araneidae might be refuted, and these characters would function as synapomorphies of linyphiids (this latter alternative is the one mapped on Figure 1). Linyphiids seem to have reduced the number of prolateral trichobothria in the male palpal tibia (character 29) from two (pimoids and outgroups in the data set) to one. However this putative synapomorphy of linyphiids might loose generality (i.e. might be refuted) in a data set with a larger sample of taxa. The same might happen to the number of retrolateral teeth on the female chelicera (character 37), which is four or more in all but one of the linyphiid taxa in the data set, and acts as putative synapomorphy for linyphiids.

The linyphiid suprategulum (character 13) is a projection of the tegulum that bears the column and through which the sperm duct passes (Saaristo (1971, 1975); Millidge (1977); Coddington (1990a)). However, the suprategulum might not be homologous across all linyphiids. The tegular projection that Blest (1979, figs 596-602) and Blest and Pomeroy (1978, figs 2, 4) call the 'suprategulum' in New Zealand mynoglenines does not bear the column (which in some cases is far from it, e.g. *Pseudafroneta*, in Blest's figure 597) and has no sperm duct going through it. I have interpreted the mynoglenines as lacking a suprategulum (*sensu* Saaristo) and coded its tegular apophysis as a structure synapomorphic for mynoglenines and not homologous to the suprategulum ('mynoglenine tegular apophysis', character 12). However, the tegular apophysis of *Haplinis* seems to be functionally analogous to the suprategulum in some linyphiids (van Helsdingen (1965, 1969); Blest and Pomeroy (1978)) in engaging the socket of the epigynal scape, but data on the functioning of the genitalia across taxa are still very scarce. The suprategulum of *Stemonyphantes* is articulated to the tegulum by means of a membranous connection (van Helsdingen, 1968:124; pers. observ.) and is different from the rest of linyphiid suprategula which are fused to the tegulum (character 13). The cladogram in Figure 1 suggests the possibility of independent origins for these two types of suprategula, and therefore questions its homology (secondary absence of the suprategulum in the mynoglenines -versus independent gains-requires one additional step).

The linyphiid embolic membrane (van Helsdingen, 1969) is not homologous to the araneoid conductor because of their different position (but see Coddington, 1990a:16). The embolic membrane (character 18) is a putative synapomorphy for all linyphiids, with the exclusion of the basal genus *Stemonyphantes*. The 'embolic membrane' *Microlinyphia* is not an outgrowth of the column, as in most linyphiids (van Helsdingen, 1986:123), but a structure 'arising from (the) membranous connection of radix, base of embolus, and dorsal side of lamella' (van Helsdingen, 1970:6). I have interpreted it as not homologous to the column-positioned embolic membranes, but the nature of this membrane remains dubious. The alternative, i.e. coding it as an embolic membrane shifted to a radical position in *Microlinyphia*, produces no change in the cladogram topology.

The terminal apophysis (character 25) is a synapomorphy for erigonines plus linyphiines, but its interpretation offers several problems. The first is its homology with its homonym in araneids (Saaristo 1971, 1975; Coddington, 1990a). Such homology is dependent, among other things, on a sister-group relationship between araneids and linyphiids (plus pimoids), but even so the homology is not obvious. *Zygiella x-notata* (which is considered here as an araneid) lacks anything

similar to a terminal apophysis, pimoids lack the radix (therefore, we do not know if they ever had such apophysis), and basal linyphiids (i.e. *Stemonyphantes* and the mynoglenines) have simple radices and no terminal apophysis. The cladogram in Fig. 1 suggests independent origins (i.e. non homology) for the terminal apophysis in araneids and linyphiids. If the embolic division of *Stemonyphantes* is interpreted as simple (and not simplified) it also suggests that complex embolic divisions in araneids and in linyphiids arose independently. This latter interpretation would question the monophyly of araneids plus linyphiids (e.g. Coddington, 1990a:14). Second, and at a less inclusive level, not all erigonines and linyphiines have a terminal apophysis. Evaluation of the homology of these apophyses requires a more detailed cladistic structure for the family (i.e. more taxa and more characters). Another radical sclerite, the lamella characteristica (character 26), is a putative synapomorphy for the linyphiines. Further support for the monophyly of Micronetini plus Linyphiini is given by the loss of metatarsus IV trichobothrium (character 40) and the position of the male during the construction of the sperm web and during ejaculation (characters 46 and 47). The phylogenetic information provided by the latter two characters should be regarded as provisional, because of the high number of missing entries for these characters in the matrix. According to Blest and Pomeroy (1978) *Haplinis* is unique among linyphiids in having an expansion of the palp prior to its locking to the female genitalia, while in the remaining linyphiids for which this trait is known the male first locks its palp to the epigynum and then expands the haematodocha. However, in a recent study on African linyphiids Scharff (1990:62) described a similar expansion prior to locking for *Neriene kibonotensis* (Tullgren). More data on the distribution of this character are needed in order to establish it as a mynoglenine synapomorphy.

Erigonine monophyly is supported by the retrolateral tibial apophysis of the male palp, the loss of the female palpal claw, and the desmitracheate tracheal system (*sensu* Millidge, 1984). In the present dataset the epigynal atrium (character 33) is the only synapomorphy supporting the monophyly of Linyphiini. An epigynal atrium is also present in the mynoglenine genus *Haplinis* (Blest, 1979:100) but absent in *Novafroneta* (Millidge 1984:241). The cladogram suggests independent origins for these two atria; its homology is therefore questionable (similar epigynal atria are also present in other linyphiids, not included here, that are not closely related to the Linyphiini; Millidge, 1984; van Helsdingen, *in litt.*). Three synapomorphies support the monophyly of Micronetini: the paracymbial apophyses, a short embolus (it also occurs in *Erigone*), and the presence of Fickert's gland in the radix.

The nature of the clypeal glands is another interesting problem in linyphiid evolution. Whether the mynoglenine sub-ocular sulci are or are not homologous to the male erigonine post-ocular sulci is a matter of debate. Mynoglenine sub-ocular sulci are found both in males and females (they are very similar in both sexes; juveniles also have functional sulci, at least in the species of *Haplinis* studied by Blest and Taylor, 1977), they do not play any active role during the courtship (at least in the species studied by Blest and Pomeroy, 1978), and they probably elaborate defensive secretions (Blest and Taylor, 1977; but this latter hypothesis has not been empirically tested, although the unique ultrastructure of the clypeal secretory cells is consistent with the synthesis of a toxic product). On the other hand, erigonine post-ocular sulci (as well as the cephalic elevations) are found (mostly) in adult males. These erigonine sulci usually have pores associated with glands that are cytologically different from those of the mynoglenine sulci (Blest and Taylor, 1977; Schaible *et al.*, 1986; Schaible and Gack, 1987), and they play an active mechanical role during the courtship (they are gripped by the female cheliceral fangs). Nevertheless, these erigonine glands are not always associated with cephalic specializations. Mynoglenine and erigonine ocular sulci can be interpreted as homologous structures within the same transformation series or as two independent developments. The available evidence is not easily interpreted in either way. The mynoglenine and erigonine sulci differ in their position, in the cytological structure of their associated glands, and in their behavioral role. It seems that the available data argue against the homology hypothesis, since they fail to meet the classical homology criteria of position and detailed similarity. Congruence with other character systems offers a powerful test of the homology hypothesis of the sulci. Blest (1979:165) argued that the most economical hypothesis (i.e. parsimonious) 'would suggest that the sulci of the mynoglenine type gave rise directly to the kind found in Erigoninae'. Mapping his hypothesis on his cladogram (*op. cit.*, p. 172, which in parenthi-

cal notation can be summarized as: Mynogleninae (Linyphiinae, Erigoninae)) requires the gain of the mynoglenine type of sulci in the common ancestor of all linyphiids, profound modifications (morphological, cytological, and behavioral) of the sulci to achieve the erigonine type of sulci (either in the ancestral erigonines or at the level of the linyphiine-erigonine ancestor) and finally the loss of the sulci (and its accompanying glands and behavior) in the linyphiines. The alternative hypothesis (i.e. non homology of mynoglenine and erigonine sulci) maps on the mentioned cladogram as two independent gains of the two types of sulci. The evolution in parallel of the erigonine and mynoglenine sulci would then account for their differences. Although the latter hypothesis is more parsimonious (in both Blest's and my cladogram) this question cannot be truly tested until more data (taxa, particularly those with any type of sulci and/or glands, and information on the glands) are included in the data set. This is due to the effect that mynoglenine and erigonine cladogram topologies might have on the optimization of the character(s) on the linyphiid cladogram. Only then we will be able to asses alternative hypotheses on the evolution of these cephalothoracic specializations.

The linyphiid tracheal system needs to be studied in detail and re-evaluated. New morphological descriptions are needed, since at least some of the available comparative data are inaccurate (see above). Millidge's (1986, figure 12) scheme for the evolution of the tracheal system in linyphiids is therefore not valid, because it is partially based on inaccurate data.

The most parsimonious hypothesis to explain the data presented in this study is the cladogram depicted in Figure 1, which suggests (as well as the three equally parsimonious alternatives that exist) relationships different from those proposed by Wunderlich (1986:106). The mynoglenines are considered here to be relatively basal linyphiids, while Wunderlich suggested them as sister to the erigonines. Both hypotheses agree on considering the pimoids and *Stemonyphantes* as the most basal clades, and on the monophyly of the Micronetini plus the Linyphiini. To use either of these two phylogenies as a classification would be premature. Wunderlich did not explicitly list the synapomorphies that define the monophyletic groups in his cladogram, synapomorphies are mixed up with diagnostic characters (some of which are not synapomorphic), and there is no mention of the genera included in each monophyletic group, even in a schematic manner. My study should be considered only a preliminary sketch of linyphiid relationships. Clearly, a much larger sample of taxa is needed before the main monophyletic groups can be established. The addition of new taxa and new characters might affect the cladogram topology presented here. As we have seen, non-homoplasious characters for wide ranges of taxa are more the exception than the rule, and different character systems often delimit conflicting monophyletic groups. When large numbers of taxa and characters are studied quantitative studies are imperative. Cladistic studies provide explicit and testable hypotheses of relationship and are recognized as the most reliable method for retrieving the phylogenetic pattern that underlies organic diversity. Not until this approach is adopted will advances in linyphiid higher classification become a reality.

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LITERATURE CITED

BLEST, A.D. 1979. Linyphiidae-Mynogleninae. Pp. 95-173. In R.R. Forster and A.D. Blest. The spiders of New Zealand, part V. Otago Museum Bulletin 5: 1-173.

BLEST A.D. & POMEROY, G. 1978. The sexual behaviour and genital mechanics of three species of *Mynoglenes* (Araneae: Linyphiidae). Journal of Zoology (London) 185: 319-340.

BLEST A.D. & TAYLOR, H.H. 1977. The clypeal glands of *Mynoglenes* Simon and some other linyphiid spiders. Journal of Zoology (London) 183: 473-493.

CARPENTER, J.M. 1988. Choosing among multiple equally parsimonious cladograms. Cladistics 4: 291-296.

CODDINGTON, J.A. 1989. Spinneret silk spigot morphology: evidence for the monophyly of orbweaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae plus Nesticidae. Journal of Arachnology 17: 71-95.

1990a. Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoidea, Deinopoidea). Smithsonian Contributions to Zoology 496: 1-52.

1990b. Cladistics and spider classification:

Araneomorph phylogeny and the monophyly of orbweavers (Araneae: Aranemorphae; Orbiculariae). Acta Zoologica Fennica 190: 75-87.

CODDINGTON, J.A. & LEVI, H.W. 1991. Systematics and evolution of spiders (Araneae). Annual Review of Ecology and Systematics 22: 565-592.

FARRIS, J.S. 1969. A successive approximations approach to character weighting. Systematic Zoology 18: 374-385.

1988. Hennig86, version 1.5. (Computer program distributed by its author, 41 Admiral Street, Port Jefferson Station, NY 11776).

GRISWOLD, C.E. (in press). Investigations into the phylogeny of lycosoid spiders and their kin (Arachnida, Araneae, Lycosoidea). Smithsonian Contributions to Zoology.

HENNIG, W. 1966. 'Phylogenetic Systematics'. (University of Illinois Press: Urbana). 263pp.

HORMIGA, G. In press. A revision and cladistic analysis of the spider family Pimoidae (New Rank, Araneoidea, Araneae). Smithsonian Contributions to Zoology

LEVI, H.W. 1981. The American orb-weaver genera *Dolichognatha* and *Tetragnatha* north of Mexico (Araneae: Araneida, Tetragnathinae). Bulletin of the Museum of Comparative Zoology 149: 271-318.

MILLIDGE, A.F. 1977. The conformation of the male palpal organs of Linyphiid spiders and its application to the taxonomic and phylogenetic analysis of the family (Araneae: Linyphiidae). Bulletin of the British Arachnological Society 4: 1-60.

1984. The taxonomy of the Linyphiidae, based chiefly on the epigynal and tracheal characters (Araneae: Linyphiidae). Bulletin of the British Arachnological Society 6: 229- 267.

1986. A revision of the tracheal structures of the Linyphiidae (Araneae). Bulletin of the British Arachnological Society 7: 57-61.

1988. The relatives of the Linyphiidae: phylogenetic problems at the family level (Araneae). Bulletin of the British Arachnological Society 7:253-268.

PATTERSON, C. 1982. Morphological characters and homology. Pp. 21-74. In Joysey, K.A. and Friday, A.E. (eds) 'Problems of Phylogenetic Reconstruction'. (Systematics Association Special Volume No. 21, Academic Press: London and New York).

PETERS, H.M. & KOVOOR, J. 1991. The silk-producing system of *Linyphia triangularis* (Araneae, Linyphiidae) and some comparisons with Araneidae. Structure, histochemistry and function. Zoomorphology 111: 1-17.

PLATNICK, N.I., CODDINGTON, J.A., FORSTER, R.R. & GRISWOLD, C.E. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). American Museum Novitates 3016: 1-73.

SAARISTO, M.I. 1971. Revision of the genus *Maro* O.P.-Cambridge (Araneae, Linyphiidae). Annales Zoologici Fennici 8: 463- 482.

1975. On the evolution of the secondary genital organs of Lepthyphantinae (Araneae, Linyphiidae). Proceedings of the 6th International Arachnological Congress (Amsterdam, 1974): 21-25.

SCHAIBLE, U. & GACK, C. 1987. Zur Morphologie, Histologie und biologischen Bedeutung der Kopfstrukturen einiger Arten der Gattung *Diplocephalus* (Araneida, Linyphiidae, Erigoninae). Verhandlungen des Naturwissensschaftlichen Vereins in Hamburg 29: 171-180.

SCHAIBLE, U., GACK, C. & PAULUS, H.F. 1986. Zur Morphologie, Histologie und biologischen Bedeutung der Kopfstrukturen männlicher Zwergspinnen (Linyphiidae: Erigoninae). Zoologische Jahrbücher (Systematik) 113(3): 389-408.

SCHARFF, N. 1990. Spiders of the family Linyphiidae from the Uzungwa mountains, Tanzania (Araneae). Entomologica Scandinavica, Supplement No. 36: 1-95.

VAN HELSDINGEN, P.J. 1965. Sexual behaviour of *Lepthyphantes leprosus* (Ohlert) (Araneidae: Linyphiidae), with notes on the function of the genital organs. Zoologische Mededelingen (Leiden) 41: 15-42.

1968. Comparative notes on the species of the holarctic genus *Stemonyphantes* Menge (Araneida, Linyphiidae). Zoologische Mededelingen (Leiden) 43(10): 117-139 .

1969. A reclassification of the species of *Linyphia* Latreille, based on the functioning of the genitalia (Araneida, Linyphiidae) I. Zoologische Verhandelingen (Leiden) 105: 1-303.

1970. A reclassification of the species of *Linyphia* Latreille, based on the functioning of the genitalia (Araneida, Linyphiidae) II. Zoologische Verhandelingen (Leiden) 111: 1-86.

1983. Mating sequence and transfer of sperm as a taxonomic character in Linyphiidae (Arachnida: Araneae). Verhandlungen des Naturwissensschaftlichen Vereins in Hamburg 26: 227-240.

1986. World distribution of Linyphiidae. Pp. 121-126. In Eberhard W.G., Lubin Y.D., Robinson B.C. (eds) 'Proceedings of the Ninth International Congress of Arachnology, Panama, 1983'. (Smithsonian Institution Press: Washington, D.C.).

WUNDERLICH, J. 1986. 'Spinnenfauna gestern und heute'. (Erich Bauer Verlag bei Quelle and Meyer: Wiesbaden).